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Effects of elevated CO_2 on the foraging behavior of cotton bollworm, *Helicoverpa armigera*

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Abstract Effects of elevated CO_2 on the foraging behavior of cotton bollworm *Helicoverpa armigera* Hübner reared on milky grains of spring wheat grown in ambient, 550 μL/L and 750 μL/L CO_2 concentration atmospheres in open-top chambers (OTC) were studied. The results indicated that: (i) elevated CO_2 significantly affected both the type and amount of food eaten by *H. armigera* reared on milky grains of ambient CO_2-grown wheat were significant higher than those for bollworm larvae reared on wheat grains grown in 550 and 750 μL/L CO_2 atmospheres; (ii) when bollworm larvae were reared on mixed milky grains from different CO_2-grown wheat (food-choice condition), larval duration increased significantly - pupal weight, adult longevity, and fecundity decreased significantly, comparing with those reared on milky grains of ambient CO_2-grown wheat, 550 μL/L CO_2-grown wheat and 750 μL/L CO_2-grown wheat respectively; (iii) significant decreases in the contents of fructose and gross protein (GP) and significant increases in the contents of glucose, amylose, total saccharides (TSC), TSC: GP ratio, free amino acids and soluble protein in the wheat grains with CO_2 rising; (iv) and selected-foraging amount/food-choice index of cotton bollworm *H. armigera* were significantly positive correlated with the contents of fructose and GP of wheat grains, but they had significantly negative relationships with the contents of glucose, amylose, TSC and TSC: GP ratio of wheat grains.

Key words elevated CO_2, foraging behavior, *Helicoverpa armigera*, open-top chamber, spring wheat

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Introduction

Atmospheric CO_2 concentration is continuously rising due to industrial development and burning of fossil fuels (e.g., coal and petroleum etc.), and is anticipated to double within 100 years (Watson *et al*., 1996; Houghton *et al*., 2001). Profound impacts of elevated CO_2 on terrestrial ecosystems, especially on chemical components and nutritional quality of plants, are expected (Luo *et al*., 1999; Penuelas *et al*., 2002). In general, elevated CO_2 increases photosynthesis, growth, yield and C: N ratio for most plant species, particularly C_3 plants (Cure & Aycock, 1986; Bazzaz, 1990; Barbehenn *et al*., 2004a, 2004b). Consequently, the interspecific interactions between plants and herbivorous insects are often altered (Wu, 1993; Bezemer & Jones, 1998).

Rising CO_2 levels may affect the feeding behavior of herbivorous insects because of the increasing of host plant C: N ratios or the changing of herbivorous insects' composition under elevated CO_2 levels. Awmack *et al*. (1996) reported that the grain aphid *Sitobion avenae* Fabricius tended to select wheat plants grown at elevated CO_2 levels, rather than those in ambient conditions. It is consistent with the results of the reproductive activity of aphid *S. avenae* sucking on different CO_2-grown wheat. The alate forms

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deposited more offspring on plants grown at 550 and 750 μL/L CO_2 compared with ambient CO_2 (Chen *et al*., 2004b). Moreover, Chen *et al*. (2005a) indicated that aphids, *Aphis gossypii* showed a significantly higher preference to colonize and oviposite on the 750 μL/L CO_2 patch compared with that in the ambient CO_2 patch, and the predator, ladybird beetle Leis axyridis consumed 3% more aphids from 1050 μL/L CO_2 treatment and 17% more aphids from 750 μL/L CO_2 patches compared with that from the ambient CO_2 patch. However, the effect of elevated CO_2 on the insect performance differed between feeding guilds (Bezemer & Jones, 1998). For most leaf-chewing insects (e.g., lepidopteran pests), elevated CO_2 causes compensatory increase in food consumption and/or reduced digestive efficiency, growth, survival rates and population abundance (Chen *et al*., 2004a, 2005c).

Cotton bollworm *Helicoverpa armigera* Hübner is one of the leaf-chewing insects and a cosmopolitan pest (Zalucki *et al*., 1986; Zalucki & Furlong, 2005). It occurs in four generations every year in northern China, the first generation damages wheat (Dong & Du, 1995; He *et al*., 1996), and the second generation migrates to hurt cotton (Luo *et al*., 1990; Wang *et al*., 1998; Ge *et al*., 2005). In this paper, the foraging behavior of cotton bollworm *H. armigera* reared on different CO_2-grown spring wheat was studied by food choice experiment in order to quantify: (i) the effect of elevated CO_2 on foraging behavior of cotton bollworm *H. armigera* via changes in the plant quality; and (ii) the relationships between the foraging amount of bollworms and chemical compositions of the ingested wheat grains.

Materials and methods

Wheat variety and growing conditions

Seeds of the local commonly used spring wheat (*Triticum aestivum* L. cv. Kehan 50) were used and sown in plastic pots (35 cm diameter × 45 cm height) filled with 8: 3: 1 (by volume) loam: cow dung: earthworm frass on March 11, 2003, and the pots were randomly put in three 4.2 m diameter octagonal open-top chambers (OTC) in Sanhe County, Hebei Province, China, 55 pots per OTC. The position of pots in each OTC were randomly changed every day to minimize the position effects within OTCs, and the controlling CO_2 levels were randomly exchanged among the three OTCs once every week to minimize differential OTC impact. The open tops of the OTCs were all covered with nylon netting to prevent insect migration. Planting density was thinned to 80 stems per pot after seedling emergence.

The atmospheric CO_2 concentration treatments were described by Chen *et al*. (2004a, 2004b), that is, 370 μL/L (ambient CO_2), 550 μL/L and 750 μL/L (double-ambient CO_2). One OTC was used for each CO_2 treatment. During the period from seedling emergence to harvest, pure CO_2 mixed with ambient air was injected into the OTCs and the CO_2 levels were monitored and adjusted with an infrared CO_2 analyzer (Ventostat 8102, Telaire Company, Goleta, CA, USA) at an interval of 20 minutes every day. The actual mean CO_2 concentrations throughout the field experiment are shown in Table 1. More details of the measure and control system of CO_2 and OTCs were described by Chen and Ge (2004) and Chen *et al*. (2005b).

Insects

From April 20 to May 10, 2003, 200 overwintering pupae of *H. armigera* were obtained by dissecting population chambers in cotton crop fields of Sanhe County, Hebei Province, China, and were stocked in a copulatory cage (30 cm length × 30 cm width × 45 cm height); moths were mating and reared with 10% sucrose solution after eclosion. Eggs were collected and stocked in a growth chamber (HPG280H, Orient Electronic Ltd Co., Haerbin City, China) at 27 ± 1℃, 60% RH (day) and 70% RH (night) and 14: 10 (L: D) hour photoperiod. Active radiation (9 000 lx) was supplied by twelve 60-watt fluorescent lamps in each chamber. After hatching, larvae were reared on a standard artificial diet (Wu & Gong, 1997).

Foraging experiment

During the milk stage of spring wheat (from May 30 to June 10), ears were harvested from the three OTCs, and

Table 1 Actual mean CO_2 concentrations (μL/L, 24 h/d) and temperature (℃, 24 h/d) in three open-top chambers from seedling emergence to harvest.

	Open-top chambers		
	Ambient CO_2	550 μL/L CO_2	750 μL/L CO_2
CO_2 concentration	382.4 ± 24.8	542.1 ± 28.4	738.8 ± 25.7
Temperature	25.9 ± 5.4	26.4 ± 4.8	26.7 ± 4.8

One-way ANOVA on temperature between three open-top chambers: $F = 0.46$, $P = 0.63$.

grains, as the food for *H. armigera*, were stocked in a refrigerator at 4℃. Newly hatched 1st instar larvae were randomly selected from the stock population and inoculated in the center of glass discs (9 cm diameter × 1 cm height), one larva per disc and 15 individuals with three replicates (i.e. total 45 larvae for the experiment). Each disc was divided into three sectors (120° per sector). Grains from three OTCs were randomly put on each sector, and labeled as A, B and C, respectively. During the foraging experiment, the grains in each disc were replaced everyday. All the discs were placed in growth chambers (HPG280H, Orient Electronic Ltd., Haerbin, China), and the growing conditions were the same as those for the stock population.

Measured indexes

Food-choice index The amount of wheat grains from each of the three CO_2-level OTCs used to feed bollworm larvae was weighed and recorded daily. Simultaneously, grains from the same CO_2-level OTC were dried in an oven at 80℃ for 72 hours to calculate water content (%) of the test grains using a gravimetric method (Douglas *et al*., 1986). The remaining grains from three CO_2-level OTCs and bollworm frass were also weighed separately for each disc, and dried in an oven at 80℃ for 72 hours to measure water contents (%) by using the same methods (Douglas *et al*., 1986). The initial and remained dry weight of test grains from different CO_2-level OTCs in each disc was calculated, and the minus value was named as selected-foraging amount (i.e. $W_{ambient}$, W_{550} and W_{750} described in the following formula of food-choice index). The dry weight of bollworm frass in each disc was also weighed and recorded daily. A modified food-choice index was obtained according to the formula described by Wu (1995):

$$\text{Food-choice index} = W_i / (W_{ambient} + W_{550} + W_{750}),$$

where i = ambient CO_2, 550 μL/L CO_2 or 750 μL/L CO_2; $W_{ambient}$, W_{550} and W_{750} are the selected foraging amounts from the three CO_2 level OTCs, respectively.

Life history indexes The ecdysis, pupation and eclosion of bollworm were checked and recorded daily. Mean relative growth rate (MRGR) was calculated by the method of Viskari *et al*. (2000):

$$\text{MRGR} = (\ln W_2 - \ln W_1)/t,$$

where W_1 = initial weight (g); W_2 = finial weight (g); t = larval duration (d).

After eclosion, bollworm moths were mating in cages (30 cm length × 30 cm width × 40 cm height) for 3 days, and then paired moths (one female and one male) were put in a plastic cup (9 cm diameter × 15 cm height) with a net cover of degreased cotton yarn to oviposit. The cotton yarns were replaced every day. Eggs reproduced in each disc were counted and recorded daily.

Nutritional constitute assay of wheat grains

Three hundred grains were selected randomly from different CO_2 OTCs, and dried at 80℃ for 72 hours to a constantly dry weight. After grinding, the grain powder was stocked in glass desiccators. The contents of fructose, glucose, amylase, total saccharides (TSC), gross protein (GP), TSC: GP ratio, and free amino acids of the grains were determined by the methods of Chen *et al*. (2004a). Soluble proteins were analyzed according to Kinney *et al*. (1997).

Data analysis

One-way analysis of variance (ANOVA) (SAS 6.12, SAS Institute Inc. USA, 1996) was used to analyze the effects of elevated CO_2 on the foraging behavior (i.e. selected-foraging amount and food-choice index) of cotton bollworm *H. armigera* reared on milky grains of different CO_2-grown spring wheat. The difference between means was compared with least significant difference (LSD) test. Test data were transformed prior to LSD-test where appropriate, to satisfy assumptions of normally, that is, the percent data (i.e. food-choice indexes) were arcsine transformed, and larval duration, pupal weight, adult longevity, and the number of eggs laid per female, were all log transformed. Moreover, Pearson correlations were also used to analyze the relationship between food-choice index (selected-foraging amount) for bollworm and chemical composition contents of milky grain of spring wheat grown in different levels of atmospheric CO_2, respectively.

Results

Effects of elevated CO_2 on foraging behavior of H. armigera

CO_2 significantly affected selected-foraging amount ($P < 0.05$) and food-choice index ($P < 0.01$) for *H. armigera*. Bollworm larvae preferred to forage the milky grains of ambient CO_2-grown wheat (Table 2). Comparing with ambient CO_2, the selected-foraging amount and food-choice index of bollworms reared in the two elevated CO_2 treatments were decreased significantly ($P < 0.05$).

Table 2 Selected-foraging amount and food-choice indexes of cotton bollworm, *Helicoverpa armigera* Hübner fed on milky grains of wheat plants grown in atmospheres with different levels of CO_2 at 27 ± 1℃.

Measured indexes	CO_2 levels (μL/L)			ANOVA
	382.4 ± 24.8	542.1 ± 28.4	738.8 ± 25.7	
Selected-feeding amount (g)	0.56 ± 0.02 a	0.45 ± 0.06 b	0.40 ± 0.08 b	$F_{2,4}$ = 6.13* P = 0.035
Food-choice index	0.40 ± 0.04 a	0.32 ± 0.02 b	0.28 ± 0.03 b	$F_{2,4}$ = 15.20** P = 0.004 5

* $P < 0.05$, ** $P < 0.01$. Different letters show significant difference at $P < 0.05$ by LSD test.

Effects of food choice condition on H. armigera as larvae fed on different CO_2-grown wheat

When the bollworm larvae were reared in a mixed diet consisting of wheat grains harvested from different CO_2 level OTCs (food-choice experiment), significant changes were observed in life history, consumption and frass, compared with those reared on milky grains of ambient CO_2-grown wheat, 750 μL/L CO_2-grown wheat (Chen *et al*., 2004a) and 550 μL/L CO_2-grown wheat (Chen 2004, unpublished data), respectively. There was significant increase in larval duration and consumption and significant decrease in mean relative growth rate (MRGR), pupal weight, moth longevity and frass excreted per larva (Table 3). Moreover, the number of eggs laid per female decreased in the food-choice experiment (Table 3).

Effects of elevated CO_2 on the nutritional constitutes of milky grains of spring wheat

With the CO_2 concentration rising, some nutritional constitutes of milky grains, such as glucose and gross protein (GP) decreased ($P < 0.05$), while some others, such as glucose, amylose, total saccharides (TSC), TSC: GP ratio and free amino acids, increased ($P < 0.05$; Fig.1). The content of soluble protein in milky grains did not change significantly when the concentration of CO_2 was raised from 550 μL/L to 750 μL/L (Fig. 1).

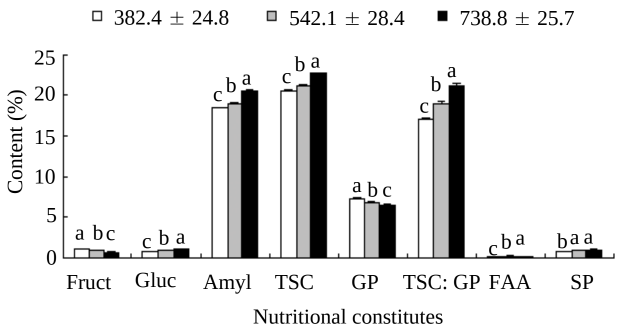

Fig. 1 The nutritional constitute content in milky grains of spring wheat grown in CO_2 levels of 382.4 ± 24.8 μL/L, 542.1 ± 28.4 μL/L and 738.8 ± 25.7 μL/L. Fruct, fructose; Gluc, glucose; Amyl, amylase; TSC, total saccharides; GP, gross protein; TSC: GP, ratio of total saccharides to gross protein; FAA, free amino acids; SP, soluble protein. Different letters indicates significant difference between treatments at $P < 0.05$ by LSD test.

Table 3 Analysis of the measured index values at 27 ± 1℃ between the food choice treatment and those treatments for cotton bollworm *H. armigera* reared on milky grains of wheat plants grown in atmosphere with ambient, 550 μL/L CO_2 and 750 μL/L CO_2 respectively.

Measured indexes		Food choice experiment	Ambient CO_2 treatment[†]	550 μL/L CO_2 treatment[‡]	750 μL/L CO_2 treatment[§]
Larval duration (day)		20.1 ± 0.9 a	17.3 ± 0.6 b	17.3 ± 1.2 b	17.3 ± 1.5 b
Mean relative growth rate (MRGR)		0.13 ± 0.02 b	0.24 ± 0.03 a	0.24 ± 0.02 a	0.24 ± 0.02 a
Pupal weight (g)	♀	0.14 ± 0.02 b	0.19 ± 0.01 a	0.19 ± 0.01 a	0.19 ± 0.00 a
	♂	0.11 ± 0.02 b	0.17 ± 0.01 a	0.17 ± 0.01 a	0.17 ± 0.01 a
Moth longevity (day)	♀	20.3 ± 1.80 b	26.3 ± 3.00 a	28.0 ± 2.00 a	30.5 ± 3.80 a
	♂	12.0 ± 2.00 b	20.0 ± 2.80 a	22.7 ± 5.10 a	24.1 ± 5.50 a
Number of eggs laid/ female		498.8 ± 57.8 a	595.0 ± 73.8 a	546.6 ± 82.5 a	518.3 ± 128.0 a
Consumption (mg)		1.42 ± 0.15 a	0.56 ± 0.10 c	0.73 ± 0.15 bc	0.82 ± 0.11 b
Frass weight (mg)		0.07 ± 0.02 c	0.14 ± 0.01 b	0.17 ± 0.02 ab	0.19 ± 0.04 a

[†, §]Chen *et al*. (2004a); [‡]Chen (2004), unpublished data. Different letters indicate significant difference between treatments at $P < 0.05$ by LSD test.

Relationship between selected-foraging amount/food-choice index for bollworm and nutritional constitute contents of wheat grains

Correlative relationships between selected-foraging amount/food-choice index and nutritional constitute contents of milky grains were examined using Pearson's correlation. Both of the selected-foraging amount and food-choice index of bollworm larvae were positively correlated with the contents of fructose and gross protein (GP) in milky grains ($P < 0.05$), and negatively correlated with glucose, amylose, total saacharides (TSC) and TNC: GP ratio ($P < 0.05$; Table 4).

Table 4 Pearson correlation analysis between selected-foraging amount and food-choice index of the bollworm larvae and food (milky grains of wheat) nutritional constitutes.

Nutritional constitutes	Selected-feeding amount (g)	Food-choice index
Fructose (%)	0.78*	0.84*
Glucose (%)	−0.75*	−0.83*
Amylose (%)	−0.72*	−0.81*
Total saccharides (TSC, %)	−0.72*	−0.80*
Gross protein (GP, %)	0.75*	0.84*
Ratio of TSC: GP	−0.73*	−0.84*
Free amino acids (%)	−0.24	−0.39
Soluble protein (%)	−0.40	−0.53

* $P < 0.05$.

Discussion

The effects of rising CO_2 on the interspecific interactions between plants and herbivore insects have been an item of great concern for the scientific community for over three decades (Bezemer & Jones, 1998; Fang *et al*., 2000; Hunter, 2001; Newman *et al*., 2003). Elevated CO_2 affects insects indirectly by altering tissue structure and chemical component contents of plants, increasing C: N ratio and decreasing foliar nitrogen (Bezemer & Jones, 1998; Hunter, 2001). The results of this study indicated that elevated CO_2 significantly affected the nutritional constitute contents of wheat grains, with significant decreases in fructose and gross protein (GP), and significant increases of glucose, amylase, total saacharides (TSC) and TSC: GP ratio. This is consistent with previous studies (Luo *et al*., 1999; Penuelas *et al*., 2002; Zhang *et al*., 2002; Barbehenn *et al*., 2004a, 2004b).

Both the selected-foraging amount and food-choice index of bollworm larvae were significantly affected by the elevated CO_2 due to the changes in nutritional constitute context of milky grains owing to rising CO_2 (Fig. 1; Table 4). Bollworm larvae preferred to forage on wheat grains grown in an ambient CO_2 atmosphere. The result was contrary to the responses of phloem-feeding insects to CO_2-mediated changes in host-plant quality, that is, preferring to feed and oviposite on wheat plants grown at elevated CO_2 levels, rather than those grown in ambient conditions (Awmack *et al*., 1996; Chen *et al*., 2004b, 2005a). This may indicate that insects from different feeding guilds respond to CO_2-mediated changes in host-plant quality in different ways (Bezemer & Jones, 1998). The cotton bollworm *H. armigera*, as a leaf-chewer, prefers to feed on ambient CO_2-grown wheat plants, contrary to the response of phloem-suckers, such as aphids.

Since the bollworm larvae have the same rearing conditions for *H. armigera* (Chen *et al*., 2004a), it is possible to make a comparison of previous studies on the life history parameters among different CO_2 concentrations. There were no significant differences in larval duration, pupal weight of both sexes and moth longevity among the three CO_2 (i.e. ambient 550 μL/L and 750 μL/L) treatments. However, significant differences were observed in the above measured parameters when bollworm larvae were reared on a mixed diet (food-choice experiment) compared with those reared on milky grains of ambient CO_2-grown wheat, 550 μL/L CO_2-grown wheat and 750 μL/L CO_2-grown wheat, respectively. Moreover, food-choice condition also caused significant increase in the food consumption per larvae and significant decrease in the frass weight per larvae; the same significant differences were also shown between 750 μL/L CO_2 treatment and ambient CO_2 treatment (Chen *et al*., 2004a). Therefore, it indicates an adverse effect on the growth, development and fecundity of *H. armigera*, when they were reared on a mixed diet, which may be due to more energy loss in the foraging behavior (Scriber & Slansky, 1981; Stearns, 1989; Slansky, 1993).

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